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Impact of climatic change on alpine ecosystems: inference and prediction

Nigel G. Yoccoz, Anne Delestrade and Anne Loison

1 Alpine climate has changed during the last decades and future changes will be even larger (Beniston, 2009). But climate does not change alone: agriculture and forestry, tourism, nitrogen deposition, invasive species are all factors that can affect alpine ecosystems. We are then faced with both the complexity of changes and of ecosystem functioning: prediction (Box 1) of global changes impact on ecosystem structure and function (biodiversity, species distribution, biogeochemical cycles) is difficult. Recent years have, however, seen rapid developments of predictive models. Our objective here is not to review what is known of the impact of climatic change on alpine ecosystems – we will use only some selected examples – but rather to project ourselves in the near future, ask some specific questions and suggest some answers: what kind of research approach is best suited to refine our projections? In other words, what kind of data and models do we need?

Box 1: Scenarios, projections, predictions, forecasts, verification, validation…: a glossary

2 What will be an alpine ecosystem in 50 years from now? To answer this question requires integrating many disciplines (climatology, social sciences, economics, ecology, statistics to quote only five) that have all their own vocabulary. For a statistician, a model makes predictions – nothing to do with magic, the model is only applied to new data, and predictions can be made for the future, another region or the past. Under the assumption that the structure and the parameters of the model apply to these new observations, it is possible to calculate the uncertainty of these predictions. In social sciences, it is often illusory to develop predictive models for which uncertainty can be estimated, and use of scenarios is common, for example within the IPCC framework. These scenarios correspond to simplified frames for the evolution of our society, and no likelihood or

probabilities are associated to them. They often project in the future recent evolutions, with changes often dependent of rather crude economic options. Similarly (but based on highly complex numerical models), climate models project in the future what is known of the climate today, but modifying some variables (such as CO_2 concentration) according to the economic scenarios. Forecast is often used for predictions which are not long-term, as for example for weather or economic forecasts, but what is long term depends on the discipline: 10 days for daily weather forecasts, some years at most in economics. All predictions or forecasts should, however, be validated. This is possible for weather forecasts – and is done routinely and using more and more elaborate tools, taking in particular forecasting error costs (Casati *et al*., 2008), but difficult if the projection is for the climate in 2060. There are then two possibilities: validate models in other regions, for example by building a predictive model of species distribution in Switzerland and validate in Austria (Randin *et al*., 2006), or validate in the past, for example by comparing climate obtained from a climate model and a climate reconstructed using proxys such as pollen and macrofossils (Kaspar *et al*., 2005). Such a validation does not lead to model verification – in other words, “all models are wrong, but some are useful” (Box *et al*., 2005) – a model can be valid or useful to make predictions even if one knows that some components of the model are poor approximations of species’ ecology.

3 To make predictions imply in most cases using quantitative models, based on equations linking what will change – climate among other factors - and variables we focus on: distribution or abundance of species (for example: where do the rock ptarmigan will survive in 100 years from now), or more functional aspects (for example, primary production or ecosystem resilience to extreme environmental events such as the drought of 2003, very severe in the Alps (Rébetez, 2004)). These models vary along an axis with purely numerical models without biological mechanisms at one end and mechanistic models, using known effects on ecosystems and projecting them in the future (Morin and Thuiller, 2009). The former models can be very efficient at describing the present, but do not usually lead to an understanding of the causes behind the changes. To base projections on such models can be unreliable. It is also more satisfying to understand rather than just predict, but it can be necessary, particularly so for management in a short-term perspective, to achieve optimal predictions without waiting for better knowledge of mechanisms which can take long time to achieve. The art is to combine the two approaches – include mechanisms when they are important and known with enough precision to lead to reliable forecasts, and to describe the rest using numerical approaches, but based on rigorous statistical criteria (Gallien *et al*., 2010). The option of building “realistic” models including all known mechanisms is not a viable one because the enormous complexity and uncertainty of such models make them useless (Oreskes, 2003).

4 We address in this paper three levels for the response to climatic change: individuals, populations and ecosystems (Stenseth *et al*., 2002). These three levels are inter-dependent, and we will show how ecosystem impacts can be derived from impacts at the individual level. However, as data and models differ among levels, we keep the distinction. The examples chosen – phenology, distribution and trophic interactions – are not exhaustive, but reveal what are the main challenges ahead.

Phenology

5 It is one of the phenomena most directly linked to temperature, even if other factors can be important (photoperiod): we are all aware that the first leaves or flowers appear earlier in a warmer spring. Earlier seasons have been described throughout the world (Menzel *et al.*, 2006; Morissette *et al.*, 2009), and mountains are no exception (Ziello *et al.*, 2009). But snow can influence the direct effect of air temperatures: plants cannot start their development before snow melting (Wipf and Rixen, 2010). An increase in winter precipitations, if it leads to an increase in snow depth, can therefore limit the impact of a warmer spring. Moreover, some species, such as migratory birds, are influenced by what is happening in their wintering or migration grounds, usually in lowlands or in southern regions, and can therefore be out of synchrony with local plants, coming too early compared to the availability of resources (Inouye *et al.*, 2000). On the contrary, if the decision to start breeding or molt (for a ptarmigan, say) depends on photoperiod, this can lead to a delay.

6 A large number of models have been developed to link plant phenology to different climatic variables – spring temperatures, but also winter temperatures as some tree species need to be “chilled” before they can start their development (Chuine, 2000). These models can be mathematically complex and require detailed temperature data, allowing calculating at the daily scale the sum of temperatures above a given threshold (degree-days). These models have been developed in lowlands – very little is known for mountain areas, and even less for alpine areas. This can be explained by the origin of phenological data, most often coming from botanical gardens or meteorological stations, which are rare in alpine regions, and focusing on species which do not reach high altitudes (most are trees, and often broad-leaved trees: Menzel *et al.*, 2006). Therefore, the majority of studies published on phonological changes in Europe or North America focus on lowlands, and the influence of snow is very rarely analyzed or discussed.

7 The CREA has therefore started the project Phénoclim, a network of stations monitoring phenology and temperatures, covering the French Alps with some additional stations in Italy and Switzerland. As Phénoclim was started in 2005, it cannot be used to build up a predictive model of phenological changes for the next 20 or 50 years, as it was done in other regions. But the first results, using the altitudinal gradients to identify climatic factors influencing important phenological events (as bud burst; see Vitasse *et al.*, 2009), suggest that snow, through its impact on soil temperature and early development, is an important driver. Trees of course burst later at higher altitudes, but the delay observed is larger than what would be expected from a simple effect of the temperature decrease with altitude: some species need a larger accumulation of degree-days to reach a given stage such as bud-burst (Pellerin *et al.*, under revision). The spring warming (particularly strong in some alpine regions: www.meteosuisse.ch) will therefore not just influence phenology directly, but also indirectly through the decrease in snow cover. We believe that developing phenological models integrating snow is needed for alpine environments. As climate scientists are developing predictive models for snow cover and depth (Beniston, 2009), the latter could be used in predictive models of phenological changes.

8 Plants are not the only organisms with their life cycles being affected by ongoing climatic changes. Birth dates for marmots or chamois, laying dates for birds, or emergence of butterflies are also impacted by climatic variation to some degree: if butterflies are more

likely to be directly influenced by spring or summer temperatures, determination of birth dates of chamois is more complex (for example because mating occurs in the fall). Arrival dates of migrating birds is also influenced by weather conditions, but often far from their breeding areas (Jonzén *et al.*, 2006). That life cycles are influenced by different factors leads to possible changes in the interactions among species, a point we detail below.

9 We now know that phenological changes represent one of the most rapid response to climatic change, but that these responses can differ greatly from one group to the next. Moreover, alpine areas have their own specificities (snow, migrating or hibernating species) which have not been integrated in most models. The lack of data in alpine regions explains in part why modeling effort has been relatively weak in this region with a more complex functioning, but recent studies and networks should lead to a better understanding of alpine specific characteristics.

Distribution

10 Models used to predict species distributions as a function of climate have developed rapidly in the last 20 years (Thuiller *et al.*, 2009). As some of the research groups working on these models study alpine species, we know in fact much on these species. Alpine species distributions are often closely linked to climate. The forest or tree line, and therefore of the tree species, is likely to be the first example that comes to mind. It is also an excellent example of human influence through land use: in the Alps, the tree line is usually below what climate alone would allow for, a well known consequence of grazing. A study in the Swiss Alps has shown that a large part of the altitudinal increase in tree line is due to a decrease in land use at high altitudes, and that the ongoing warming has not contributed much (Gehrig-Fasel *et al.*, 2007).

11 Species distribution models, also called niche models, are conceptually relatively simple: on one hand predictive variables, preferably climatic variables having a direct influence on organisms, on the other data on species distributions, often from atlases or surveys. A large number of statistical models exist to link these two types of data (se BIOMOD; Thuiller *et al.*, 2009). A large number of studies have compared these models without reaching a consensus: it is not because a model is better at describing species distribution today that it will be better at predicting future changes. This problem is well known in climatology – models that describe best mean temperatures and precipitations today are not the best models to describe the changes observed during the last 30 or 50 years (Räisanen, 2007). We have too few data on changes in distributions during the 20th century to perform similar comparisons.

12 Studies on alpine species distributions focus mainly on plants because available data are often of much better quality (data on alpine insects for example are very poor). Distribution of alpine species is well described by climatic variables, such as temperature of the coldest (frost) and warmest months (which can limit growth, in particular for woody species), evapotranspiration and summer precipitations. The climatic warming expected for the next 50 or 100 years (+4 to +6 ºC for summer temperatures in the Alps) would lead therefore to distributions moving upwards, often by 500 to 1000 meters (Randin *et al.*, 2009). But many factors can invalidate these projections: 1) Models fitted to present distribution assume that climate and distribution are at equilibrium, i.e., present distribution reflects present climate. For example, absence of a species in a given area is not due to a slow colonization. Most predictions indeed assume that plants can "follow"

climate changes, i.e. disperse instantly to new favorable habitats. This is a reasonable assumption for short distances, but it may be more difficult if it implies dispersing from one mountain range to another, or if changes are very quick: including dispersal can therefore lead to different predictions (Engler *et al.*, 2009). 2) Alpine environments are heterogeneous over short distances, but many models use rather large-scale gridded data (10x10 or 50x50 km). Average climate over large areas do not include this heterogeneity, and use of data at smaller scale (100x100 m or less) lead to different future distributions (Randin *et al.*, 2009). 3) Climatic factors are not the only factors influencing species distributions – land use (grazing), management of large herbivores, nitrogen deposition can also play a role, but it is both difficult to predict their changes and their influence.

13 Another component limiting predictive models is data quality, for both climate and species distributions. As for phenological studies, there are few weather stations in alpine regions, and models use climate data interpolated from these stations (Zimmermann and Kienast, 1999). Even if such interpolations reconstruct the main patterns (altitudinal gradients or outer-inner regions in the Alps), they smooth local heterogeneities linked to the complex topography of the Alpine range. Distribution data are also often fragmentary, and not sampled according to known criteria. Species distribution models fitted to such data can differ from those obtained using data acquired using rigorous sampling designs (Albert *et al*., 2010).

14 Birds and mammals are primarily influenced by habitat characteristics rather than directly by climate. A bird like the Alpine chough needs cliffs to breed and alpine meadows to feed. Cliff distribution is not affected by climate, but the distribution of alpine meadows depends on climate (through changes in tree line) but also on land use changes (e.g., colonization by rhododendron). Effects of climate change are therefore hard to infer if both direct and indirect (through habitat changes) effects are not understood. This can explain why altitudinal distribution of birds in the Italian Alps has not changed much (Popy *et al*., 2010).

15 Changes in mammalian distributions as a consequence of climatic changes have been less studied than in plants (e.g., Levinsky *et al*., 2007). Some species are limited by climatic factors – it could be the case for the lower limit of the alpine marmot, and snow duration is a limiting factor for some species. But to take an example of habitat being more important than climate, the snow vole, a small rodent found in the Alps at up to 4000 m asl, has a name poorly reflecting his preferences since it can also be found at the sea level in Croatia! Its distribution is linked to presence of scree with relatively large boulders, and those are found only in some mountain regions. The direct influence of climate on distribution and abundance of large mammals has been relatively minor, particularly so in Europe. Indeed, the indirect role of climate on habitats, land use and harvest management (hunting) has been much greater. Large herbivores have been intensively harvested for meat, trophy and as competitors of domestic ungulates up to mid 20^{th} century. It is only after a general discussion of the status of the flora and fauna that national parks first, and thereafter management plans outside protected areas, have allowed for an increase in abundance and distribution. It is therefore difficult to assess the direct impact of climate on the high densities of large herbivores in mountain regions, as well as their increase at higher and higher altitude. Studies of population dynamics show that species respond differently to snow depth, spring phenology or summer drought. While the chamois is sensitive only to winters with extreme snow

depths, ibex and roe deer seem to respond negatively to winters with rather averaged snow depths.

16 By continuously monitoring both distributional changes and mechanisms limiting populations locally, we should be able to identify the relative importance of direct (snow, winter harshness, summer temperature) and indirect effects (quality and phenology of resources) on geographical and numerical changes of different species. It is particularly important to understand demographic mechanisms leading to species extinctions at low altitudes, and colonization at high altitudes - these mechanisms are likely to differ. For plants for example, competition could explain extinction of population at low altitudes, whereas temperature and dispersion could limit colonization at high altitudes (Zimmermann *et al*., 2009). There are very few species for which colonization and extinction mechanisms are known.

Ecosystems and trophic interactions

17 Research on ecosystems is done following two approaches, the first focusing on energy and matter flows (e.g., C and N), the other focusing on interactions among species, and in particular those defining the trophic web of the ecosystem. We will discuss here only the latter, and specifically interactions among plants and herbivores (“herbivory”) and herbivores and carnivores (“predation”). As for direct and indirect effects of climate on species demography, changes in CO_2 concentrations can have both direct (on plant growth and C assimilation, i.e., flows of matter in the ecosystem) and indirect effects (through resistance to herbivory; Lau and Tiffin, 2009) on ecosystems, and we make this distinction in order to simplify the discussion.

18 Climate can influence trophic interactions first through changes in phenology. For an herbivore – a chamois as well as a caterpillar – quality and quantity of vegetation change rapidly through the spring/summer. If quantity increases gradually until a maximum is reached in the middle of the summer, quality is often much higher early during plant growth. A caterpillar or a young chamois will therefore achieve higher growth if they can match it to the period with highest quality of vegetation. Alpine environments differ since mobile organisms can follow phenological changes, for example by moving upwards in spring (Albon and Langvatn, 1992). By doing so, they can compensate for an earlier phenology. On the other hand, less mobile species with a slower response to warming than vegetation can show a mismatch with their resources. The direction of the effect can vary with altitude. Some species seem to match the phenology of their resources only for a specific temperature and snow pattern – the “optimal” band for these herbivores will move upwards with warming. This seems to occur with an insect pest of birch forests in mountains of North Norway, which is now impacting forests close to the tree line, with potential consequences for the evolution of the tree line in this area (Hagen *et al*., 2007). A insect pest of larch, however, has seen its outbreaks disappear in the last decades in Engadine, for the first time in 1,200 years, probably as a consequence of the present mismatch between the insect life cycle and its host, the larch (Esper *et al*., 2007).

19 Predation – by wolf on chamois or by stoat on vole – can also be directly influenced by climate, in particular by snow conditions (Stenseth *et al*., 1998). This will be exacerbated by different sensitivities of prey to snow: a chamois, with its interdigital membrane, move faster on snow than a roe deer or a mouflon, which sink in deep or powder snow. In

addition to the increased energetic costs associated with movement, the differences in ability to move on snow will also influence predation risk. More snow in the winter season could therefore benefit large predators, which could in the future be negatively affected by a decreasing snow cover. The recolonisation dynamics of large predators in the Alps is quick, made easier by the abundance of their prey. If climatic changes are unlikely to be the major cause of the ongoing geographical expansion of large predators, they impact their prey (population size and relative abundance of the different species) and may therefore affect large predators' population dynamics in a complex, but important way. It is only by jointly studying the different trophic levels, from plants to large herbivores to predators that we will be able to disentangle the direct effects of climate and the indirect effects associated to trophic interactions among species.

20 Understanding impact of climate on trophic interactions is difficult because these interactions vary spatially – for example the match between herbivores and plants described above – and the climatic variables with an ecological impact, such as snow quality, are not directly measured but have to be calculated, often with a large uncertainty, from other variables such as temperature and precipitation. Snow is also difficult to manipulate experimentally (it is easier with temperature or CO_2 concentrations) even if some studies have done it, but at very small spatial scales (a few m^2; van der Wal *et al.*, 2000; Wipf and Rixen, 2010). It is therefore not surprising that very few studies have convincingly demonstrated a direct impact of snow on interactions such as predation, which often act at large spatial scales (Garrott *et al.*, 2009).

Conclusions and perspectives

21 Almost by definition, climate determines where alpine ecosystems are found – any change in climate will force them to move, and to disappear if species cannot follow (by dispersal) their climatic niche or if their niche is not within the altitudinal limits of the regions of interest (Thuiller *et al.*, 2005; Randin *et al.*, 2009). The first models linking species and climate, mostly applied with success to plants, have identified the important climatic variables, such as summer and winter temperatures but also evapotranspiration. The quality of model predictions has been checked in the field either by using models to find new populations of rare species (e.g., *Eryngium alpinum* in Swiss Alps (Guisan *et al.*, 2006)) or by transferring them to other alpine regions (Randin *et al.*, 2006). That the quality is highly variable means that distribution models need to be refined, by including mechanisms at the individual and population levels, trophic interactions among species and ability of species to respond to changes (Hoffmann and Willi, 2008). The integration of these mechanisms in models describing the impact of climate and climatic changes require, however, that data have been collected in a consistent way (i.e., they can be compared at similar spatial and temporal scales), and taking into account the large spatial variability of environmental conditions of alpine ecosystems. The current network of observations and experiments covers only a very small part of this variability and results cannot be generalized to other alpine ecosystems. Moreover, such a network should include snow measurements, such as snow hardness (Yoccoz and Ims, 1999; Kausrud *et al.*, 2008) and snow permeability for respiratory fluxes, in order to better understand the role of snow in ecosystem functioning. Setting up such a network, combining intensive observational/experimental studies of mechanisms and extensive studies validating predictions derived from intensive studies, should be a major objective if we want to

better predict how alpine ecosystems will look like in 50 or 100 years, and if our management decisions can affect their evolution towards preferred states.

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ABSTRACTS

Alpine ecosystems will be greatly impacted by climatic change, but other factors, such as land use and invasive species, are likely to play an important role too. Climate can influence ecosystems at several levels. We describe some of them, stressing methodological approaches and available data. Climate can modify species phenology, such as flowering date of plants and hatching date in insects. It can also change directly population demography (survival, reproduction, dispersal), and therefore species distribution. Finally it can effect interactions among species – snow cover for example can affect the success of some predators. One characteristic of alpine ecosystems is the presence of snow cover, but surprisingly the role played by snow is relatively poorly known, mainly for logistical reasons. Even if we have made important progress regarding the development of predictive models, particularly so for distribution of alpine plants, we still need to set up observational and experimental networks which properly take into account the variability of alpine ecosystems and of their interactions with climate.

Les écosystèmes alpins vont être grandement influencés par les changements climatiques à venir, mais d’autres facteurs, tels que l’utilisation des terres ou les espèces invasives, pourront aussi jouer un rôle important. Le climat peut influencer les écosystèmes à différents niveaux, et nous en décrivons certains, en mettant l’accent sur les méthodes utilisées et les données disponibles. Le climat peut d’abord modifier la phénologie des espèces, comme la date de floraison des plantes ou la date d’éclosion des insectes. Il peut ensuite affecter directement la démographie des espèces (survie, reproduction, dispersion) et donc à terme leur répartition. Il peut enfin agir sur les interactions entre espèces – le couvert neigeux par exemple modifie le succès de certains prédateurs. Une caractéristique des écosystèmes alpins est la présence d’un manteau neigeux important et pourtant l’influence de la neige reste relativement mal connue, en particulier pour des raisons logistiques. Même si nous avons fait des progrès importants dans le développement de modèles prédictifs, surtout pour ce qui est de la répartition des plantes alpines, il reste à mettre en place des réseaux d’observations et d’expériences permettant de mieux tenir compte de la variabilité des écosystèmes alpins et des interactions avec le climat.

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